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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIX. POSTCRANIAL MATERIALS OF THE CYNODONTS *PROBELESODON* AND *PROBAINOGNATHUS*

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ABSTRACT. Descriptions are given of postcranial materials of *Probelesodon* and *Probainognathus* and a restoration of *Probelesodon lewisi* is attempted.

Because of the phylogenetic position of the cynodont therapsids as the probable ancestors of mammals, their structure is of great importance in the story of vertebrate evolution. A number of excellent studies have been made of cranial structures of cynodonts. As regards the postcranial skeleton, there have been numerous descriptive papers, but few which have attempted a broad study of cynodont skeletal materials from an evolutionary or functional viewpoint. Early essays of this sort were those of Watson (1917), Gregory and Camp (1918), and Romer (1922); a recent comprehensive work is that of Jenkins (1971; cf. also Jenkins, 1970).

Postcranial remains of African cynodonts have been comprehensively studied and summarized by Jenkins (1971); some data on *Permocynodon* of Russia have been given by Konjukova (1946). Of the South American cynodonts, descriptions of gomphodont skeletons have been given by Bonaparte (1963) for *Exaeretodon*, and by Jenkins (1970) for *Massetognathus*, and Huene (1944) has described a limited amount of postcranial material of *Traversodon*. For the carnivorous cynodonts of South America, all so far published has been the description of a partial skeleton of *Belesodon* by Huene (1944), and of a limited amount of material of *Chiniquodon* by Romer (1969).

The purpose of the present paper is to place on record such data as are available on the postcranial skeleton of the car-

nivorous cynodonts of the Chañares Formation — *Probainognathus* and *Probelesodon*. Together with their relatives, *Chiniquodon* and *Belesodon*, from the Santa Maria Formation of Brazil, they include the latest in time and most advanced of therapsids leading in a mammalian direction. As Jenkins has noted (1971), the postcranial skeleton of cynodonts shows in general a remarkable consistency of pattern, and hence little novelty is to be expected from the description of the Chañares genera. Collection and preparation of *Probelesodon* and *Probainognathus* were made possible by grants from the National Science Foundation.

POSTCRANIAL MATERIAL OF
Probelesodon lewisi

A major source of information is MCZ 3781 (field no. 79), the remains of a nodule that contained a nearly complete and mostly articulated specimen of this form, with a skull approximately the size of the type. This is preserved as a slab, prepared on both surfaces. Photographs of the two sides (which we will call the obverse and reverse sides) are shown in Figures 1 and 2. Outlines of the materials seen on the two surfaces are shown in Figures 3 and 4. Figures 3 and 4 were derived from the photographs and, owing to perspective, the two are not completely superposable. Unfortunately, some parts of the specimen were lost before collection; further, the specimen had undergone considerable weathering and penetration by grass roots, with the result of obscuring much detail and rendering interpretation difficult.

MCZ 4002 (field no. 98), in addition to a good skull, included a fair amount of mostly disarticulated postcranial material; this material is, in general, in better shape than that of MCZ 3781. Several other concretions include postcranial materials that may be of *Probelesodon*, but for the most part such materials either add little to the data available in MCZ 3781 or MCZ 4002 or are of doubtful assignment. We may note, however, that MCZ 3801 includes a mélange of bones, certain of which rather surely pertain to *Probelesodon*, notably a pair of excellent femora.

Axial skeleton. At burial the specimen constituting MCZ 3781 appears to have had a complete vertebral column, articulated for the most part. However, before collection, a considerable portion of the dorsal vertebrae had been lost, leaving



Figure 1. Obverse side of the slab, MCZ 3781, containing a skeleton of *Probelesodon lewisii*. Slightly less than $\frac{1}{3}$ natural size.



Figure 2. Reverse of the slab shown in Fig. 1.



Figure 3. Diagram of the structures on the obverse side of the slab shown in Figs. 1 and 2. Slightly less than $\frac{1}{3}$ natural size. Abbreviations for Figs. 3 and 4: *l*, left; *r*, right; *cl*, clavicle; *f*, femur; *fib*, fibula; *h*, humerus; *ic*, interclavicle; *i*, ilium; *is*, ischium; *r*, radius; *sc*, scapula; *S1*, first sacral; *S5*, fifth sacral; *t*, tibia; *u*, ulna.

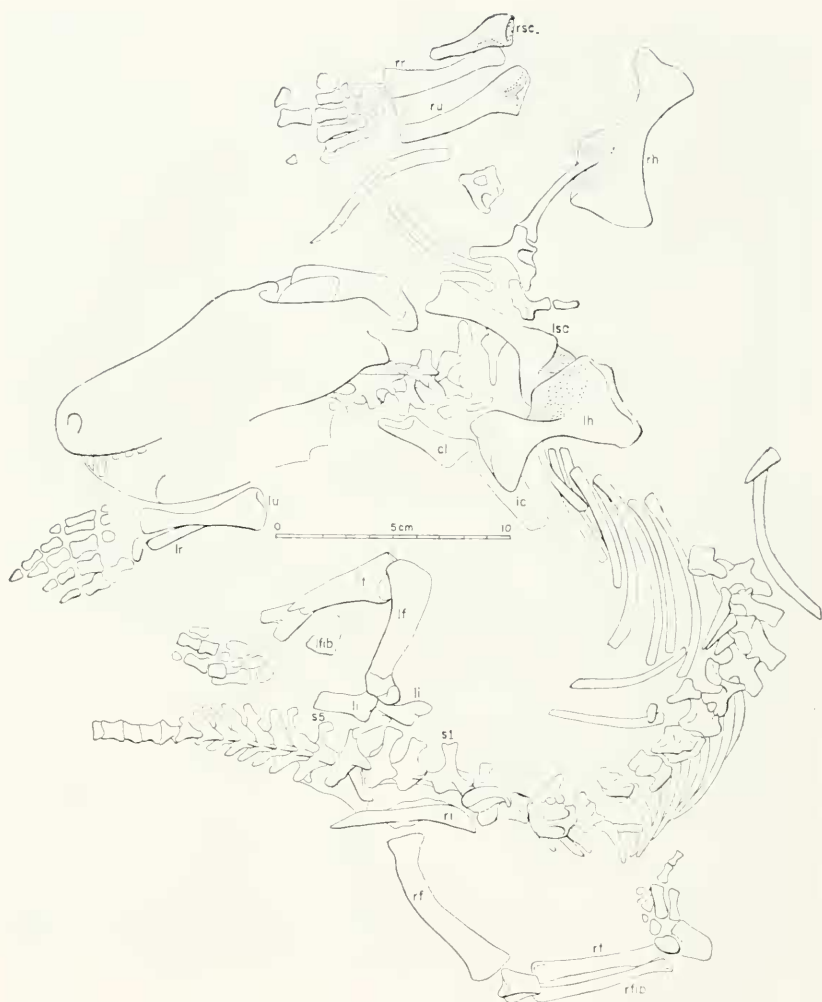


Figure 4. Diagram of the reverse side of the same slab. Slightly less than $\frac{1}{2}$ natural size. Abbreviations as in Fig. 3.

a small number of cervical vertebrae present anteriorly, then, following a gap, posterior dorsals, "lumbar," sacrals and part of the tail. Although the articulated condition of the posterior part of the column and the forward continuation of a rib series in seemingly natural position indicates that much of the column was articulated at the time of burial, it is obvious that the column had been broken at about the posterior end of the cervical series. Several isolated vertebrae, obviously from the region of the break, are present above and behind the skull.

It is impossible to be certain of the exact presacral vertebral count. As noted below, there is some question as to the position of the first sacral, but the articulated series anterior to this appears to include 14 posterior dorsals and "lumbar." For the most part the ribs associated with these vertebrae are preserved, and anterior to the vertebrae present, this rib series is continued for eight segments further to the 22nd segment anterior to the sacrum. The most anterior rib is not complete at its head, but has a moderately long shaft, and hence can be no farther forward than the posterior end of the cervical series. If 27 presacrals—a typical cynodont number—were present, this rib would pertain to vertebra 6. Since presumably the anterior cervical ribs were short, no more anterior position for this rib seems probable and we have hence assumed for purposes of restoration the typical count of 27 presacral vertebrae.

In general the preservation of the vertebrae present is not good, but as far as can be seen the structure is of the general cynodont type. Remains of three vertebrae are present close to the back end of the skull. The most anterior vertebra preserved has a neural spine (broken above) of considerable length anteroposteriorly, suggesting that we are dealing with the axis. Little more can be made out as to details of structure on the three further cervicals present in MCZ 3781 except for the presence of normal zygapophysial regions, well developed transverse processes slanting outward, backward and downward, and in two of the three, neural spines that are relatively narrow anteroposteriorly (the other—apparently the fourth in this series—appears to have a widened spine). Isolated vertebrae that appear to be cervicals are present in MCZ 4002. As preserved, the centra are subcircular in end view, with a diameter of 11–12 mm, and a central length of perhaps 10 mm. Transverse processes are well developed and extend strongly out from the arch bases.

Posterior cervicals and much of the dorsal region is missing

in MCZ 3781, although represented by a few scattered vertebrae. A number of dorsal vertebrae are present in MCZ 4002. Those best preserved have central lengths of about 12 mm, and height of centrum of 12–13 mm. They are deeply biconcave; the centrum, as seen in end view, is oval in outline, with a width somewhat less than the height. Both anterior and posterior margins of the centra are somewhat thickened; presumably the capitulum was carried on the anterior rim, but there is little indication of a discrete articular facet. The transverse processes are stout but short, extending but little outward beyond the level of the arch base, and face strongly downward. The posterior zygapophyses are almost directly above the base of the transverse processes; anteriorly the arch bases extend far forward, so that the spine extends upward about opposite the front margin of the centrum.

Of the series of 14 presacrals preserved in MCZ 3781, and mainly visible on the reverse surface of the slab, the second to fourth are seen in side view and are fairly well preserved. The neural spines are relatively short, rising to about 15 mm above the level of the zygapophyses, and broad anteroposteriorly. Centrum lengths are 12–13 mm. Beyond this point the vertebrae are seen from above, and the neural arches and spines are for the most part absent, revealing the neural canal on the surface of the slab. The series is continuous, except for the last two presacrals, which are disarticulated and damaged.

Beyond this point the sacrals and anterior caudals are articulated. Here the vertebrae are seen from above and somewhat to the left side. Eleven caudals and part of a twelfth are present. The neural arches, still well developed on the posterior sacrals, decrease in height and become more slender as we continue along the caudal series; the transverse processes, as preserved and seen on the left, likewise decrease in length posteriorly. Length of centra, about 12 mm in the sacrals, decreases to about 8 mm on the last caudal preserved. On the obverse side are seen the rounded ventral surfaces of some of the vertebrae in the series. Beneath the articulated caudal series are obscure remains of additional caudal vertebrae. On MCZ 4002 is found a series of seven articulated caudals, five of which are well preserved. The centra have lengths of 8 mm each; they are apparently somewhat compressed vertically. The height of the centra is about 5 mm; the neural spines are very short, and as preserved there is little trace of any transverse process. It seems certain that we are dealing with elements distal to the

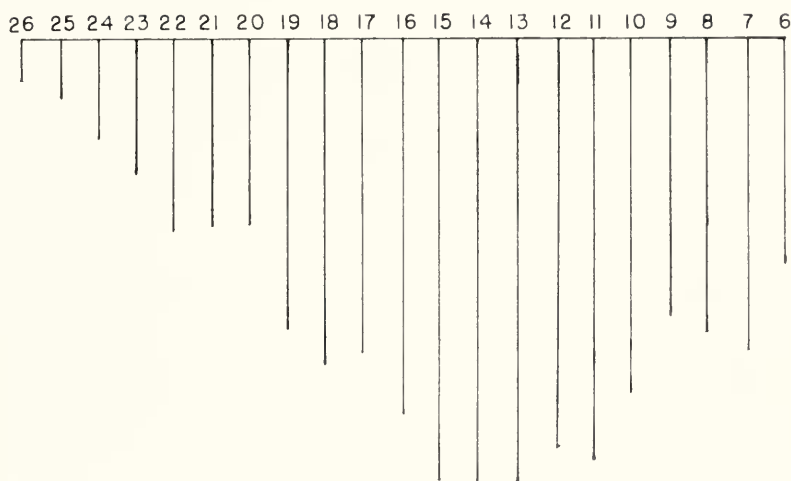


Figure 5. Lengths of right ribs of *Probesodon lewisi*, MCZ 3781, from presumed vertebra 6 to 26. Measurements are direct between the two ends of the parts preserved; rib heads are complete only on ribs 14 and 15. $\times 2/3$ natural size.

tail "stump" seen on the slab, which strongly suggest the presence of a fairly long tail.

No interpretable remains of anterior cervical ribs are preserved. Of ribs of the left side, a few dorsals are present in isolated fashion on the reverse surface of the slab. Posteriorly, a few stumps of left rib are present in the posterior dorsal-lumbar series; these have a broad head but rapidly decrease to the base of a slender shaft. There is no indication of the interlocking expansions seen in various other cynodonts.

The ribs of the right side are better preserved. Only on two ribs, which we interpret as presacrals 14 and 15, are the heads preserved; these are expanded proximally for capitular and tubercular attachments to the vertebrae, but taper rapidly distally, with no trace of proximal overlapping expansions. A proximal series of right ribs, commencing with that which we assume pertained to vertebra 6, are seen on both obverse and reverse surfaces posteriorly. The ribs attributable to vertebrae in the posterior presacral series are seen on the reverse surface, their heads concealed beneath the vertebrae. In Figure 5 we have plotted the lengths of ribs as preserved (measured directly between the two ends). Although we cannot be sure how much

has been lost proximally or distally in most cases, we see a reasonable distribution in lengths, with an increase to a maximum in the anterior dorsal region followed by a gradual decrease as we enter the lumbar region and approach the sacrum.

On MCZ 4002 a number of dorsal ribs are preserved in their entirety, including the heads; they are similar in nature to numbers 14 and 15 on the slab and appear to be mid-dorsals of both sides with average lengths of about 10 cm. Although the usually imperfect nature of transverse processes makes difficult the interpretation of the orientation of ribs to the backbone, the rib structure strongly suggests a broad, barrel-shaped abdomen.

The lumbar ribs as preserved are slender (except for the presumed first presacral) and although the heads are concealed beneath the centra, there obviously was none of the interlocking found in the lumbar series of certain other cynodonts.

In the sacral region some seven ribs on the left side show distal expansion (the first broken off from its vertebra). As the length of the associated right ilium indicates, five members of this series are sacrals; but which five? Possibly incorrectly, we assume that the first (whose vertebra is disarticulated from the sacral-postsacral series) is the last presacral (and we have used this assumption in making a count of presacral vertebrae). The first four, particularly, of the assumed sacral series are expanded at their distal surfaces for iliac articulation; two sacrals are visible in ventral view, which better shows this prominent distal expansion. A slender rod of bone, extending forward, is attached without evidence of sutural separation to the outer end of the presumed fourth left sacral; this appearance, however, is probably due to the peculiar type of preservation in this specimen, and this rod is perhaps a fragment of the left ilium.

Limbs and girdles. Remains of the shoulder girdle are present in MCZ 3781. The interclavicle is present, and on the obverse are the lower ends of the two clavicles. The interclavicle as preserved (slightly incomplete anteriorly) measures 57 mm in length. A better preserved interclavicle (slightly incomplete distally) is present in MCZ 4002 (Fig. 6b). This is of similar size, with a length of 59 mm, a width of 33 mm across the head, and, following a constriction, to a width of 11 mm back of the head, a modest increase in width distally. The structure is that typical of cynodonts in general. The anterior "quadrants" for clavicular reception are deeply incised; a median keel is present between these quadrants but there is little de-

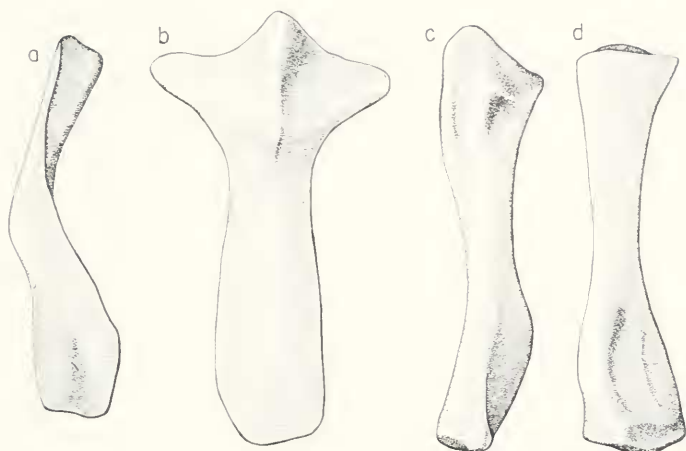


Figure 6. *Probelesodon lewisi*, a, left clavicle in lateral view; b, interclavicle in ventral view; c, ulna; d, radius of right side seen from extensor surface. All from MCZ 4002. $\times 1$.

velopment of a median ridge more posteriorly. The left clavicle is well preserved in MCZ 4002 (Fig. 6a). It is of typical cynodont build. Its length, measured directly between the ends, is 51 mm. The relatively thin shaft curves about 45° between proximal and distal ends. The dorsal end is somewhat expanded and excavated medially for acromial apposition. A well-defined ridge descends the posterior margin of the shaft and continues on to the posterior margin of the ventral expansion for articulation with the interclavicle.

Of the primary girdle in MCZ 3781, an obscure fragment of the left scapula is present; the girdle of the right side is present, but is poorly preserved and incompletely seen (Fig. 7). On the reverse side is visible the glenoid region and incomplete coracoids, in poor condition; on the obverse is the medial surface of the scapular blade. This is, as in other chiniquodonts, unusually tall and narrow, with a length (probably incomplete) from the glenoid articulation with the coracoid of 55 mm, and a width at mid-height of 11 mm. The exposed medial surface of the blade is strongly convex in the transverse plane and obviously the external surface was strongly ridged longitudinally on both front and back margins. In MCZ 4002 a scapular blade was present, but is represented by little but an impression

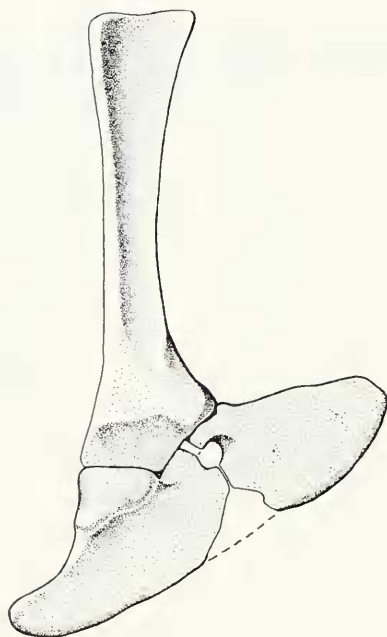


Figure 7. *Probelesodon lewisi*, right scapula and coracoids; the anterior coracoid poorly preserved, the acromial region of the scapula incomplete. From MCZ 3781. $\times 1$.

indicating that it was elongate and slender. Both coracoids are present, the posterior element complete and well preserved; the anterior coracoid is incomplete. In MCZ 3801 there is a scapular blade of *Probelesodon* type, narrow and deeply concave, externally with strong ridges posteriorly and (especially) anteriorly. As preserved, the blade is 48 mm tall, 12 mm wide at the summit, with the width decreasing to 6 mm below. Unfortunately, the scapula is incomplete ventrally, but there was obviously little acromial development and no indication of any beginning of a supraspinous surface.

Both humeri are present in MCZ 3781, and are essentially complete although somewhat crushed, and a good left humerus is present in MCZ 4002 (Fig. 8). The bone in general corresponds well with that of typical cynodonts, as described in detail by Jenkins (1971). Lengths of the humeri of MCZ 3781 as preserved are 72 and 66 mm, that of MCZ 4002 68 mm. The

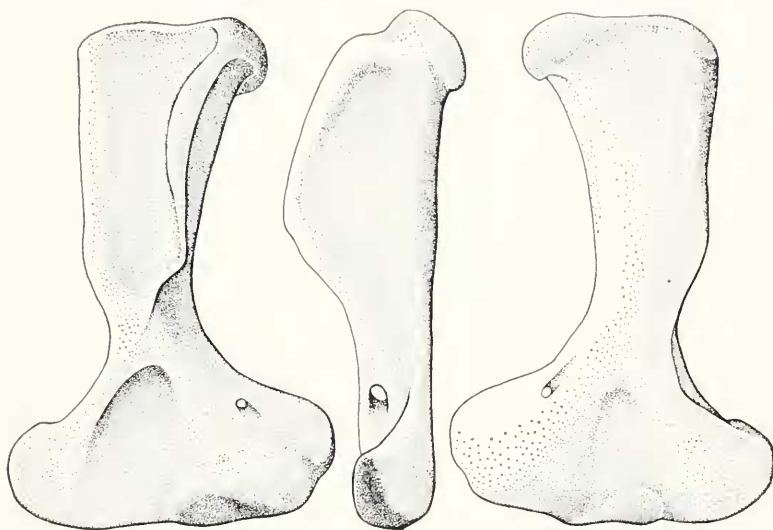


Figure 8. *Probesodon lewisi*. Right humerus in distal ventral, lateral, and distal dorsal views. From MCZ 4002. $\times 1$.

head of the bone is unusually expanded anterodorsally, so that the articular area extends into a "lip" overhanging the antero-proximal corner of the dorsal surface. The deltopectoral crest is somewhat more expanded than in typical cynodonts. The distal end of the bone is unusually broad; its width in MCZ 4002 is 43 mm, thus being about 63 percent of the length, in contrast with lower figures in most cynodonts. This increased width appears to be associated with a greater expansion than usual of the entepicondyle. On the ventral distal surface the areas for radial and ulnar articulations are well ossified in MCZ 4002.

In MCZ 3781 the right radius and ulna and left ulna and partial radius are present, but poorly preserved. In MCZ 4002 the right radius and ulna are well preserved (Fig. 6, c, d). In this specimen the radius has a length of 53 mm, the ulna 56 mm. Both bones conform well to typical cynodont structure. The radius is essentially columnar in shape, but as preserved somewhat flattened between extensor and flexor surfaces. Proximally the bone is expanded and deeply cupped for humeral articulation. Distally the width of the bone is increased toward the medial margin and thickened on the flexor surface to make



Figure 9. *Probelesodon lewisi*, right ilium and ischium, composite, MCZ 4002 and MCZ 3781. $\times 1$.

possible a broadly oval distal surface for carpal articulation. As in *Thrinaxodon*, a ridge, perhaps for biceps attachment, is present proximally on the flexor surface; a flattened area at its summit was presumably for apposition with the ulna. A ridge with a rounded summit descends the distal third of the medial margin, presumably marking the boundary between extensor and flexor muscle areas.

The ulna has the typical cynodont pattern. As usual, the olecranon is unossified except for its base, the sigmoid notch, represented only by its basal portion. At the expanded dorsal end of the bone the medial area is somewhat concave for radial apposition; lateral to this area a pronounced ridge is present proximally, fading out rapidly below. The proximal part of the flexor surface is markedly concave, bounded externally by a distinct ridge. Below, the shaft of the bone narrows, to be only moderately expanded distally for carpal articulation. Deep to the transverse plane of the shaft, however, a very strong ulnar crest is present, as in other cynodonts; this is conspicuously developed along the distal half of the bone.

Remains of the manus of both limbs are present in MCZ 3781, but in poor condition. Little certain data can be made out concerning the carpus, except for the presence of three promi-

nent distal carpals. All metacarpals are present on the left side, four on the right. Exact measurements are meaningless, owing to the imperfect nature of the material, but the average length of metacarpals II-V is about 18 mm. A limited number of poorly preserved phalanges are present but in no case is there a complete digit. The digits are, however, sufficiently preserved proximally to show that the vestigial "extra" phalanges present in primitive cynodonts were absent.

In MCZ 3781 the incomplete upper margin of the left ilium is seen on the reverse side of the slab; the vertically oriented complete right ilium is seen on the margin of the slab, and a nearly complete left ilium is present in MCZ 4002 (Fig. 9). The iliac length is about 70 mm. For the most part the structure is typical of that of cynodonts generally, but the posterior part of the blade is much more slender than in most cynodonts, suggesting that *Probelesodon* is advancing toward the mammalian condition of forward migration of the gluteal musculature. The right ischium is present in MCZ 3781, and has a normal cynodont form. Except for the area of iliac articulation of the right pubis, there are no identifiable remains of the pubis in available material.

Hind limb material is poorly preserved in MCZ 3781. Only the proximal part of the left femur is present and the right femur (with a probable length of about 80 mm) is badly crushed and broken. Only fragments are present of the left tibia and fibula. The right tibia and fibula are present but in such poor condition that little can be said except that they appear to conform generally to the usual cynodont pattern. As preserved their lengths are 74 mm and 63 mm (the fibula is incomplete proximally).

In the mélange of material in field number 188 (MCZ 3801) are two well-preserved cynodont femora which seem quite surely to belong to *Probelesodon lewisi* (Fig. 10). With a length of 63 mm each, they represent an animal smaller than MCZ 3781, but they are too large to pertain to *Probelesodon minor* or *Probainognathus*, and they differ in structure from the gomphodonts in the fauna. In nearly all respects these femora are closely comparable to the "*?Cynognathus*" femur illustrated by Jenkins (1971, fig. 48) — even to the presence, part-way down the shaft, of a groove of unknown nature. These femora, however, differ markedly from all hitherto described cynodont femora in the position of the greater trochanter. In all cynodonts hitherto described the greater trochanter lies some

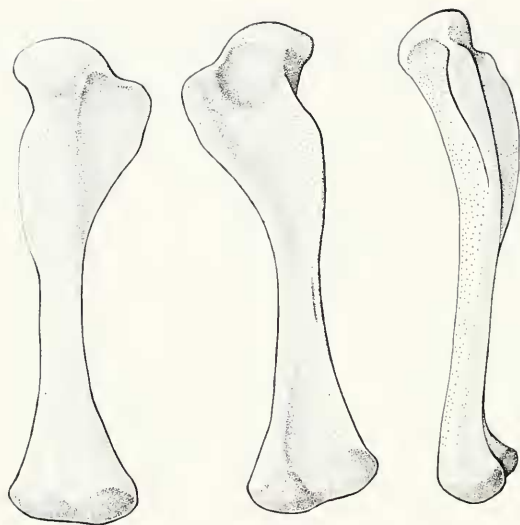


Figure 10. *Probelesodon lewisi*, left femur in dorsal, ventral and medial views. From MCZ 3801. $\times 1$.

distance down the posterior margin of the femur and faces as much laterally as proximally. In this specimen it is placed definitely farther toward the proximal end of the bone and its somewhat expanded tip faces nearly directly proximally. We have here a position splitting the difference between typical cynodonts and the mammalian condition. A femur of the chiniquodontid *Chiniquodon* described by Romer (1969, fig. 9C) shows a somewhat comparable proximal movement of the greater trochanter, but the specimen is not too well preserved.

The feet are poorly preserved. Of the left foot, a few disarticulated metatarsals, phalanges, and tarsal remains are seen on the reverse side. The right foot is nearly complete but difficult to interpret. Astragalus and calcaneum can be made out on the obverse side. Two complete and two incomplete metatarsals are present; the two complete — perhaps the third and fourth — are 17 mm in length as preserved. Although too much reliance should not be placed on measurements of such poor material, it would appear that here, in contrast to certain other cynodonts, front and hind feet were of approximately equal size. A number of phalanges are present, but except for

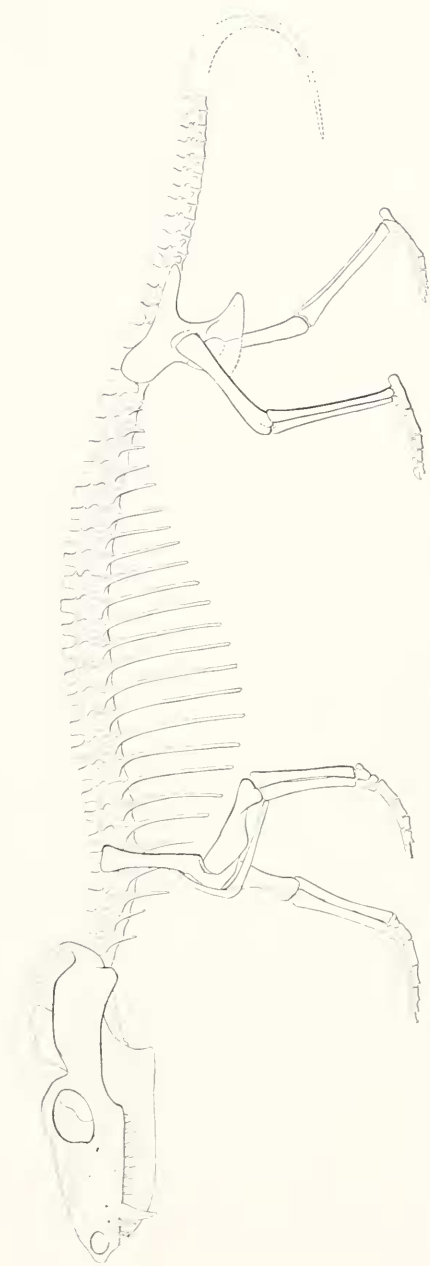


Figure 11. Restoration of *Probesodon levisi*, $\times 1/4$. As noted in the text, various elements are absent or poorly preserved, including pubis, distal phalanges, cervical ribs and vertebrae, etc.

the certain presence of two phalanges on supposed digit IV (and the obvious absence of "vestigial" phalanges), we cannot be sure of their arrangement.

Restoration. On Figure 11 we have attempted a restoration of the skeleton of *Probelesodon*. We believe that this restoration gives correctly the general appearance of the animal, although, as noted in the description above, knowledge is lacking in a number of regards, such as cervical ribs, the distal portion of the tail, the pubis, and the distal phalanges; even the probable presacral count of 27 vertebrae is uncertain. The body was surely stockily built, and although we have included in the tail only those vertebrae in MCZ 3781, the evidence indicates that *Probelesodon* (and not unlikely other cynodonts as well) had a tail of rather good length. A notable departure from the situation in many cynodonts is the almost complete absence of the overlapping of the ribs, seen at its height in *Thrinaxodon*. This type of structure has been discussed by Jenkins (1971: 76ff); unless we assume that such a late cynodont as *Probelesodon* has evolved independently from the very base of the cynodont stock, the situation, as Jenkins believes, is one in which there has been a return to "normal" rib structure.

Presumably such cynodonts actively pursued their prey, but their limbs would seem to have been relatively inefficient for speedy locomotion as compared with later mammals or contemporary archosaurs (although an improvement over the pelycosaur condition). As in early tetrapods generally, the hind legs were longer than the fore, the combined length of femur plus tibia being about 30 percent greater than that of humerus plus radius. Again, as in primitive forms generally, the podials are longer than the epipodials; the humerus is about 30 percent longer than the radius, the femur about 15 percent longer than the tibia.

Probelesodon may be compared with a canid, *Vulpes*, of similar size, and with presumably somewhat comparable habits. We may use as a crude base for comparison the length of dorsal vertebrae (approximately the same length in *Vulpes* and *Probelesodon*). To give a rough estimate of comparative limb length we may use the length of humerus and radius for the front leg, of femur and tibia for the hind leg. In *Vulpes* this front leg measurement is 19 times the length of a dorsal vertebra, in *Probelesodon*, little longer than the length of nine vertebrae. The hind leg of *Vulpes* is 21 vertebrae long, of *Probelesodon* 12 vertebrae. It is immediately obvious that for speedy loco-

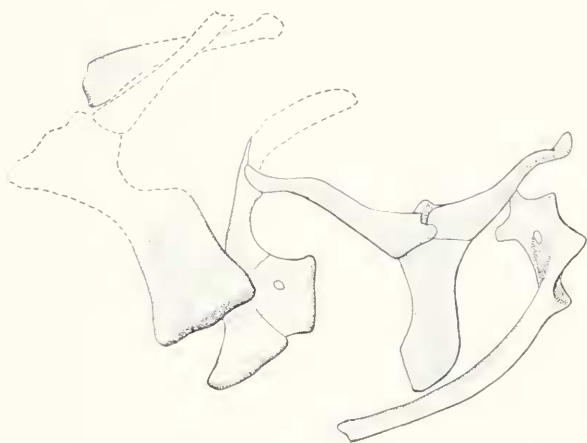


Figure 12. One surface of a block containing material of the shoulder region and front leg presumably belonging to *Probelesodon minor*. On this surface are seen the clavicle and interclavicle, most of the primary girdles, and part of the left humerus and ulna. The left scapulocoracoid is seen in external view, extending dorsally as far as the acromion. The right scapulocoracoid is seen in posterior view. MCZ 4164. $\times 1$.

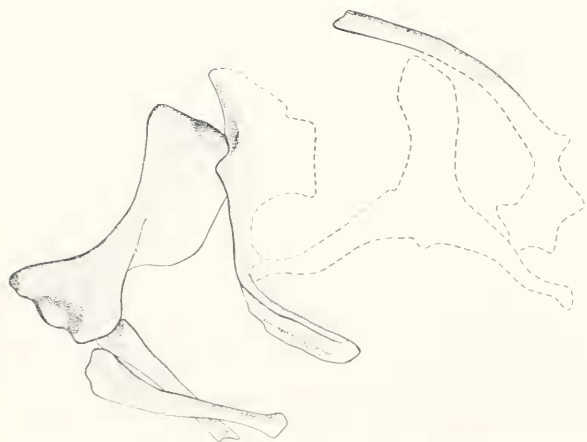


Figure 13. The opposite side of the block seen in Fig. 12, showing the left humerus, ulna, incomplete radius and part of the primary girdle. $\times 1$.

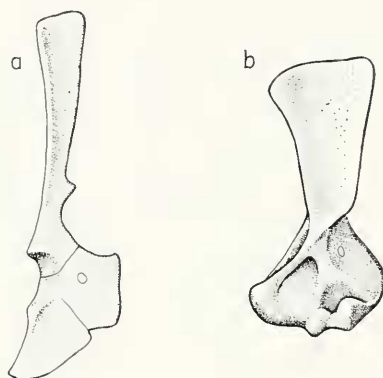


Figure 14. *Probelesodon minor*. *a*, external view of the right scapulo-coracoid; *b*, ventral view of the left humerus. MCZ 4164. $\times 1$.

motion, the limbs of *Vulpes* are far superior to those of *Probelesodon*. The contrast is still stronger if it is noted that *Probelesodon* had not completed the shift from the sprawled pelycosaurian limb position to the fore-and-aft mammalian pattern. Carnivorous cynodonts are still moderately abundant in the early Middle Triassic Chañares beds, but become rarer in the formations succeeding this horizon; meanwhile there are appearing various thecodonts of a seemingly more sprightly nature, and it is not to be wondered at that carnivorous cynodonts were reduced in competition with these rivals.

POSTCRANIAL MATERIAL OF *Probelesodon minor*

There is no positive association of postcranial materials with skulls of *Probelesodon minor*. However, in field number 40, a nodule containing a "mixed grill" of material, there is present the pectoral region of a small cynodont (MCZ 4164) which is of a size appropriate for this form and in which the scapula is of the unusually tall slender type seen in *Probelesodon lewisi*. It is highly probable that MCZ 4164 pertains to *P. minor* (Figs. 12, 13, 14).

On one surface of the block there is preserved an articulated pair of clavicles and the interclavicle. The clavicles, about 28 mm in length, are gently curved ventromedially from the presumed acromial articulation. The shaft is slender; there is

a slight expansion proximally at the acromial articulation, and a greater distal expansion, so that the two clavicles cover the anterior quadrants of the head of the interclavicle. The shaft exhibits a marked posterior "twist" below the acromial region. The interclavicle, slightly imperfect posteriorly, has a length of 31 mm. It has a typical cynodont shape — relatively broad and flat, with an anterior expansion for reception of the clavicles, a modest narrowing behind the head, and a distal expansion. The longitudinal ridge is little developed.

Both primary shoulder girdles are present. As in *Probelesodon lewisi*, the scapula is tall and very slender, with a height from the glenoid fossa of 38 mm, and a width at half-height of but 4.5 mm. The upper end widens to about 8 mm; below, it widens again to a distinctly developed acromial process (present on one scapula, broken off on the other). The scapula is curved longitudinally to about 45° from summit to glenoid fossa. It is strongly concave externally in cross section, with both anterior and posterior borders outturned — the former more strongly so. There is no development of a supraspinous fossa. At its base the posterior margin thickens to present a well-developed upper portion of the glenoid cavity, which appears to have faced nearly directly ventrally in life. The anteroposterior breadth of the scapula increases ventrally to give a broad area of articulation with the two coracoids. Sutures between the scapula and the coracoids are not clear. The posterior coracoid is incomplete on the left girdle; as preserved on the right side, it is of normal cynodont type. The posterior coracoid bears the lower half of the glenoid; it appears to extend to a relatively greater distance posterolaterally than in typical cynodonts, with a V-shaped surface, somewhat convex in cross section. The anterior coracoid is of unusual shape, in apparent contrast to that of *P. lewisi*. It attaches to the anterior edge of the scapula, and its upper margin curves strongly forward from this point, reinforced by a thick strut of bone internally. The anterior margin of the bone is broad and essentially a straight dorsoventral line, sharply set off from the upper and lower margins. The procoracoid foramen is large. A notch on the ventral margin indicates the point of division between anterior and posterior elements.

Both humeri are present, and radius and ulna are preserved on the right side. These elements conform to the general cynodont pattern, and differ from those in *P. lewisi* mainly in a more slender build correlated with smaller size. Humeral

lengths are 37 and 35 mm; proximal widths 17 mm and 16 mm; distal widths 19 mm. As in *P. lewisi* the deltopectoral crest is highly developed. The slender radius is incomplete distally; its length as preserved is 25 mm, the width of the head 6 mm. The ulna is 30 mm in length, its width proximally 8 mm, distally 5 mm. As usual in cynodonts, the olecranon is unossified.

The block of material in which this shoulder region is imbedded includes considerable further bony material; it is, however, quite uncertain that any of it belongs to this same form, and some of it certainly does not.

POSTCRANIAL MATERIALS OF *Probainognathus jenseni*

Because of the advanced nature of *Probainognathus* (at least in the type of jaw articulation) a description of the postcranial skeleton of this genus would be of considerable value. Regrettably, little can be done. In no case is postcranial material articulated with a *Probainognathus* skull. In a number of concretions containing skull materials of this genus there is present cynodont postcranial remains that may pertain to this genus. But since such concretions usually include a mélange of materials of different forms, attribution of specific elements to *Probainognathus* is in general highly questionable.

In one instance, however, pectoral and pelvic assemblages can be reasonably assigned to *Probainognathus* (Figs. 15, 16, 17). As mentioned earlier, Chañares field number 40 is a concretion including some remains of *Massetognathus*, some thecodont elements and a shoulder region described above as probably belonging to *Probolesodon minor*. Still further, however, it includes (MCZ 4021) a shoulder region of a small cynodont definitely differing from that of *Probolesodon minor* and appropriate in size for *Probainognathus*, and, nearby, a pelvic region also of appropriate dimensions.

The scapula of this specimen is quite different from that of *Probolesodon*, being relatively short and broad. Its height is 28 mm, the distal width 10 mm. The external surface is concave in cross section but anterior and posterior borders are not as sharply outturned as in *Probolesodon*. There is a well-developed acromion. The ventral anterior portion of the bone is not completely preserved, but there is a well-developed area extending forward just below the acromion, suggesting the

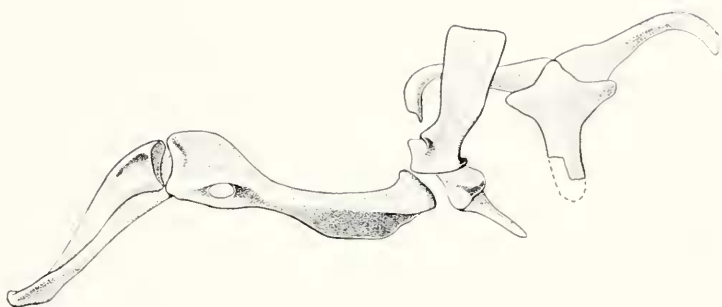


Figure 15. Shoulder girdle and front limb material of a specimen probably pertaining to *Probainognathus jenseni*. MCZ 4021. $\times 1$.

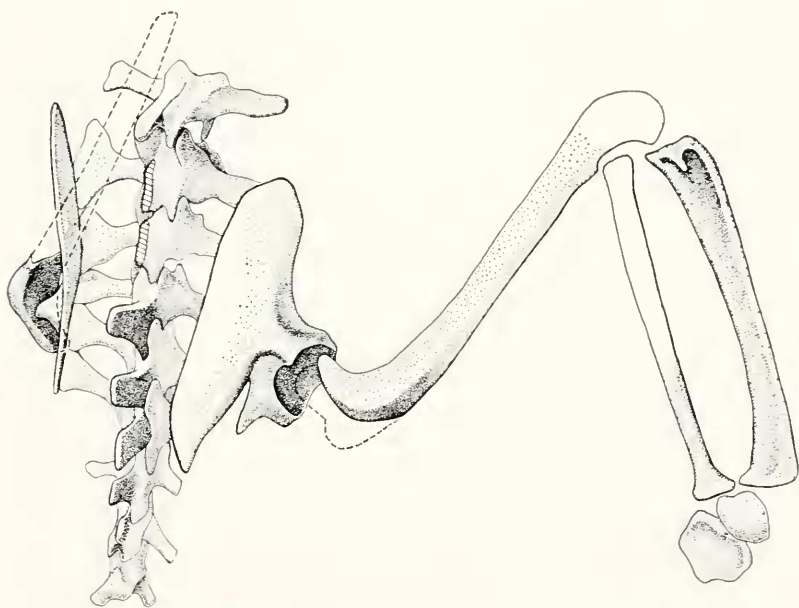


Figure 16. Pelvic region and hind leg material as seen on a block perhaps pertaining to *Probainognathus jenseni*. MCZ 4201. $\times 1$.



Figure 17. Left femur and acetabular region of the peivis as seen on the opposite surface of the block illustrated in Fig. 16. $\times 1$.

initiation of a supraspinous fossa. The posterior coracoid (seen from the upper surface) is present, extending 19 mm back from its articulation with the anterior coracoid. This latter element, partially concealed within the block, extends well forward, with an anteroposterior length of about 13 mm. The coracoid foramen is unusually large, but this may be due to accidents of preservation or over-preparation. Well-preserved clavicles and a nearly complete interclavicle are also present, the three articulated. These dermal elements are of normal cynodont structure. The interclavicle, as preserved, is 26 mm long and is relatively shorter than in *Probelesodon minor*.

The left humerus is complete with a length of 49 mm. It is unusually long and slender, the length being nearly half again that of *Probelesodon minor*, an animal of roughly similar size. The entepicondylar foramen, as prepared, is of unusually large size. Both radius and ulna of the left side are complete, with lengths of 35 mm and 34 mm, respectively. As usual, there is little ossification of the olecranon.

Various other limbs and axial skeletal elements are present in the block close to this girdle and limb assemblage, but there is no guarantee that any of them pertain to the same animal.

Not far removed from this shoulder assemblage are articulated remains of the pelvic region and hind legs of a small cynodont. There is here even less guarantee that this material is assignable to *Probainognathus* than in the case of the shoulder region, but the elements present definitely differ from those of the Chañares gomphodonts, and to some degree differ from

those of *Probelesodon*; hence they quite probably pertain to the present genus.

An articulated series of vertebrae includes the last presacral, five sacrals and four proximal caudals. The transverse processes and ribs of the last presacral are developed in much the same fashion as the sacrals, and are somewhat expanded distally, but show no evidence of connection with adjacent elements. The first sacral is obviously the strongest of the series and most expanded distally, the further sacrals decreasing in strength posteriorly.

The left and right ilia have lengths as preserved of 37 mm and 42 mm respectively. Unfortunately, their upper margins are imperfect, so that the possible contrast between the expanded anterior portions and narrower posterior portions of the ilia cannot be clearly made out. The acetabulum is deeply excavated and the supra-acetabular buttress is strongly developed. There are no remains of pubis and ischium other than the areas immediately adjacent to the acetabulum.

The right femur is nearly completely preserved; the left (seen mainly on the under surface of the block) is incomplete distally. The length of the right femur (slightly imperfect at its head) is 58 mm; the bone is quite slender, the shaft width at mid-length being only about 4 mm. The head is well seen on the left femur on the under surface of the block. As in the femur attributed to *Probelesodon* the greater trochanter is somewhat more proximally placed than in most cynodonts, but is not as thickened nor as laterally divergent as in that form, nor is there any distinct separation of trochanter from the articular surface of the head. There is no line of division of the intertrochanteric fossa from the more distal portion of the ventral surface. The lesser trochanter is highly developed and extends far down the shaft.

The right fibula, with an apparent length of 47 mm, is represented for much of its length by an impression only. The slender tibia has a length of 51 mm, with a width at mid-length of but 4 mm. As preserved the shaft is strongly concave in transverse section. Astragalus and calcaneum are imperfectly preserved.

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